Vol. 158, No. 3 June, 1980

THE

BIOLOGICAL BULLETIN

PUBLISHED BY THE MARINE BIOLOGICAL LABORATORY

Reference: *Biol. Bull.*, **158**: 271–282. (June, 1980)

PATTERNS OF SEXUALITY, ASEXUAL REPRODUCTION AND RECRUITMENT IN SOME SUBTIDAL MARINE DEMOSPONGIAE

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Although there have been few careful studies on forms of sexuality in sponges, it is clear that sponge reproduction follows a number of patterns. Sponge species may have separate sexes (Chen, 1976) or partially separate sexes with varying numbers of hermaphroditic individuals (Elvin, 1976; Fell, 1976a). Other species are hermaphroditic, producing sperm and oocytes simultaneously (Sarà, 1961; Simpson, 1968; Chen, 1976), sequentially in the form of protogyny and protandry (Sarà, 1961, 1974; Diaz, 1973), or alternating sexes (Gilbert and Simpson, 1976). Sequential changes in sex may occur during a single reproductive season (Sarà, 1961) or over consecutive years (Diaz, 1973). Other characteristics of sexual reproduction that must be considered are: 1.) whether the sponges are viviparous with embryogenesis occurring within the adult, or oviparous with oocytes or zygotes shed into the sea, and 2.) whether sexual products are released synchronously or asynchronously in individuals or the entire population (Reiswig, 1976). In addition, a number of forms of asexual reproduction are found in sponges; for example, gemmule formation, budding, and fragmentation of the adult.

In only a few studies have gamete populations been quantified (Elvin, 1976; Fell, 1976a) or reproductive output related to larval release and settlement (Fell, 1976a; Fell and Jacob, 1979). The survival patterns of sponge larvae remain largely unknown.

One reason for the lack of reliable studies on sponge reproductive patterns is the difficulty of monitoring natural populations. Most intertidal sponges are subject to considerable physical disturbance, which affects their patterns of settlement, growth and reproduction (Wells, Wells and Gray, 1964; Elvin, 1976). Long-term monitoring of these populations is often difficult because of fluctuating abundances of the sponges. In some species, small size makes regular cutting of tissue samples difficult (Fell, 1970, 1974). However, subtidal sponge populations are not so subject to physical disturbances, and, as many of the species

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Library of Congress Card No. A38–518
(ISSN 0006–3185)

are long-lived (Dayton *et al.*, 1974; A. L. Ayling, 1978a), such populations can be sampled regularly by divers.

A second reason for the paucity of reliable studies is lack of procedures by which the type of reproduction may be rigorously established. Rather than sampling the same individuals regularly, over long periods, most studies have involved only sampling of the general population. This procedure by itself inadequately describes not only gametogenic cycles but often the type of sexuality.

The object of this study was to establish the reproductive pattern of 10 species of Demospongiae from the shallow subtidal waters off northern New Zealand. In addition, the reproductive output of the species was related to recruitment rates in the natural habitat and on artificial surfaces. If the young sponge successfully settled and survived through the first month of its life it was considered in this study to have been recruited into the population. Two groups of sponges were selected for the study: thinly encrusting ceractinomorph species, and structured tetractinomorph species such as spheres, fingers and massive spreading forms. These latter sponges are referred to as discrete species because they are easily recognizable as individuals in the field, whereas the thinly encrusting species were frequently fragmented. The reproductive patterns found in these species are discussed in the light of the ecological consequences of the various products produced.

Materials and Methods

The sponges investigated were located in two subtidal sponge dominated communities near the Leigh Marine Laboratory on the east coast of northern New Zealand (36°16′S: 174°48′E). Tissue samples of the thinly encrusting species were collected from "beach canyon," a steep-walled canyon 12 m in depth on the exposed northeast side of an island. These sponges covered 46% of the walls of the canyon and were regularly grazed on by the abundant urchin *Evechinus chloroticus*. They were also subject to heavy surges during storms. Tissue samples of the discrete sponges were collected from the "sponge garden," a flat rock platform covered by a thin layer of sediment at 18 m depth. Here, sponges covered only 14% of the substratum but were numerous and subject to very little disturbance (A. L. Ayling 1978a).

The abundance of the sponge species is given in A. L. Ayling (1978b) but the following nomenclatural changes have been made: *Polymastia granulosa* = *Polymastia* sp., *Cicocalypta penicillus* = *Polymastia* sp. (yellow), *Hymedesmia lundbecki* = *Stylopus* sp. and *Tedania* sp. (pink) = *Stylopus* sp. (pink).

Permanent buoys were set up to serve as reference points for mapping the locations of six individuals of each species. Each sponge was marked by hammering a nail bearing a numbered Dymo tape tag into the rock bottom beside the sponge. Small tissue samples of all marked sponges were taken fortnightly from June, 1976, to November, 1978, to establish reproductive periods and forms of sexuality. Counts of the numbers of reproductive elements were taken from two individuals per species throughout the reproductive period by cutting five sections from each tissue block and then relating the number of reproductive elements in the section to the area and thickness of the embedded tissue. The sponges appeared to be unharmed by the sampling procedure.

Tissue samples from large species were taken from several locations within the body of the sponge to check that single samples were representative of activity throughout the sponge. When most or all of these regularly sampled sponges were reproducing, a larger random sample of 25 or more sponges was collected, with records of the size of each sponge, to investigate activity in the entire population. Tissue samples were collected in small partitioned plastic containers and preserved in Bouins fixative. Sections were cut at 6 μm and stained with Erlich's Haematoxylin (30 min) and Eosin.

During the reproductive period, large pieces of tissue were collected and placed in running sea-water aquaria for observation of the number of larvae released per day per unit of tissue and the time the larvae took to settle. Sponges producing buds were individually tagged and the number of buds released over time recorded. The settlement and recruitment of larvae and buds on settlement plates, on cleared bare rock areas and in the natural habitat were monitored monthly using the following techniques: In both study areas asbestos board settlement plates, 0.0625 m square and 5 mm thick, were bolted to the rock each month. Also in each area five 0.0625-m squares were cleared of all encrusting organisms with a chisel and a wire brush and monitored over 2 years. In the natural habitat, eight 0.0625-m-square areas were set up in each area and monitored for 2 years. Additional information on discrete sponge recruitment was obtained from ten 1-meter-square areas of natural habitat in the "sponge garden." A 10-meter-square area was marked out and random pairs of numbers used to locate each quadrat. Then the outline of all sponges in each quadrat was traced onto acetate sheets using Chinagraph pencils. These drawings were repeated 1 year later. Additional information on larval recruitment in "beach canyon" was collected from 46 0.0625-m squares of natural habitat photographed at 3-month intervals. Small knobs of epoxy cement were used to mark out the corners of the quadrats.

Results

Reproductive patterns in thinly encrusting ceractinomorphs

Stylopus sp. This orange sponge was the most abundant species in "beach canyon," forming extensive encrusting patches up to a meter in diameter and 5 mm thick, with smaller fragmented pieces surrounding the central bodies. *Stylopus* sp. reproduced over the summer months from late December or early January to the end of April. In the first year of the study, only three of the six continuously sampled sponges reproduced. In the following year, however, all the sampled sponges were active. This increase in the number of sponges reproducing was also reflected in the larger population samples, where at least 92% ($N = 70$) of sponges were active in 1978, while in the preceding year only 53% ($N = 50$) had been active.

Stylopus sp. is a simultaneous hermaphrodite which incubates its larvae. Early in the reproductive period spermatocytes appeared in numbers of up to 100 per mm^3. Then fertilized embryos appeared in numbers of up to 0.2 per mm^3 along the base of the sponge (Fig. 1A). Bright orange larvae emerged from single sponge patches over a period of approximately 2 months and were released at a rate of 1–4 per cm^3 of tissue per day. The larvae were spherical, 392 by 407 μm in size and covered with cilia except at the posterior pole, which was bare.

Stylopus sp. (*pink*). This thinly encrusting pink sponge was moderately abundant in "beach canyon," where some patches covered areas of over a meter square. *Stylopus* sp. (pink) is a simultaneous hermaphrodite similar in its re-

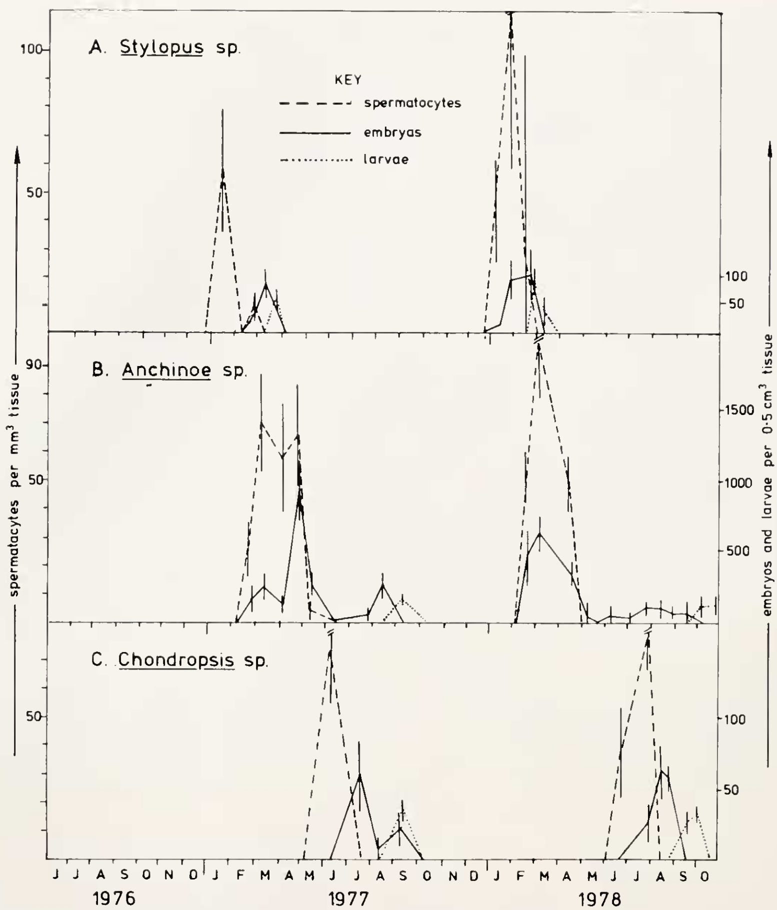

FIGURE 1. Abundance of reproductive elements in three species of thinly encrusting sponge. The data is derived from marked individuals that were continuously sampled. Vertical lines in the figures indicate plus or minus one standard error of the mean.

productive characteristics to the previously described *Stylopus* sp., both reproducing over the same summer months and producing similarly colored and shaped larvae. All six regularly sampled *Stylopus* sp. (pink) reproduced in both years of the study, but in the larger population samples only 39% (N = 41) reproduced in 1977 and in the following year, 67% (N = 70). All sizes of patches of this species were involved in reproduction. In some patches there were two episodes of spermatogenesis, with up to 100 spermatocytes per mm³ tissue. Then embryos appeared in numbers of up to 0.2 per mm³ tissue. Larvae emerged from single patches over a period of approximately 2 months and were released at a rate of 0.6–2 per cm³ tissue per day. Larvae were 240 by 210 μm in size and covered with cilia except for the posterior pole, which was bare.

Anchinoe sp. This pale yellow sponge was uncommon in "beach canyon" and usually occurred as small patches in rock crevices. The reproductive period of *Anchinoe* sp. extended over most of the year, from February to November, and in both years of the study all the regularly sampled sponges except one reproduced. This latter sponge was a very small patch and produced sperm only in 1978. In the first year of the study at least 60% ($N = 15$) of the total population reproduced, in the second year at least 73% ($N = 15$) were active.

Anchinoe sp. is a simultaneous hermaphrodite which incubates its larvae. Sperm were present for the first 4 months only. Fertilized oocytes then developed for a period of 4 or 5 months and ciliated larvae finally appeared in the last 3 months (Fig. 1B). The reproductive products were located throughout the body of the sponge, spermatocytes in numbers of up to 100 per mm^3 and the very small embryos in numbers of up to 2 per mm^3. The pale yellow larvae were 179 by 146 μm in size and released at a rate of 5.4–20 per cm^3 tissue per day.

Chondropsis sp. The fragmented patches of this sandy sponge were abundant along the base of the "beach canyon" walls. *Chondropsis* sp. reproduced from early June to late September and all the regularly sampled sponges reproduced each year although in the second year all except one were extensively damaged by a violent storm in July. At least 36% ($N = 30$) of the larger sample reproduced in 1977 but only 25% ($N = 25$) reproduced in 1978.

Chondropsis sp. is a simultaneous hermaphrodite that incubates its larvae. Sperm were produced in the first few weeks of the reproductive period. Then embryos were found for the next 4 months, with ciliated larvae appearing in the last month. Spermatocytes in numbers of up to 70 per mm^3 and embryos in numbers of 0.1 per mm^3 tissue were located in patches throughout the mass of the sponge (Fig. 1C). The yellow larvae were released at a rate of 0.2–3 per cm^3 tissue per day and were shaped like flattened discs (as in *Halisarca*, Chen, 1976), 1.6 mm in diameter.

Reproductive patterns in discrete tetractinomorphs

Ancorina alata. This massive gray sponge could grow to a size of 2 square meters but was uncommon in the "sponge garden." *Ancorina alata* reproduced from early February to early June. All six continuously sampled individuals reproduced in both years of the study but in the larger population sample only 40% ($N = 60$) of sponges were reproductively active in the first year and 53% ($N = 28$) in the second year. *A. alata* is apparently gonochoric and oviparous. Over 2 years the sexual identity of each of the regularly sampled sponges was maintained and in each sponge there were frequently two cycles of sperm and oocyte production during the reproductive period (Fig. 2A). At the end of each cycle gametes were released over a week. The ratio of males to females was 1 : 5.3, the majority of the reproductive population thus being female. An examination of sections taken from various parts of the bodies of single sponges showed that the entire sponge was involved in production of only one type of gamete. In male sponges spermatocytes were located near the gray surface tissue in numbers of up to 1000 per mm^3 and in female sponges oocytes were located in the white body tissues in low numbers; about 50 per mm^3.

Polymastia sp. Polymastia sp. is a bright yellow spherical sponge abundant in the "sponge garden" with individuals up to 20 cm in diameter occurring singly or in groups of three or more. The beginning of the reproductive period of *Polymastia* sp. shifted over the 2-year period from August in 1976 to January in 1978. But both periods ended in May. In both periods all of the continuously sampled sponges reproduced. In the 1978 reproductive period 96% ($N = 156$) of sponges reproduced while in the pervious summer 56% ($N = 50$) were recorded

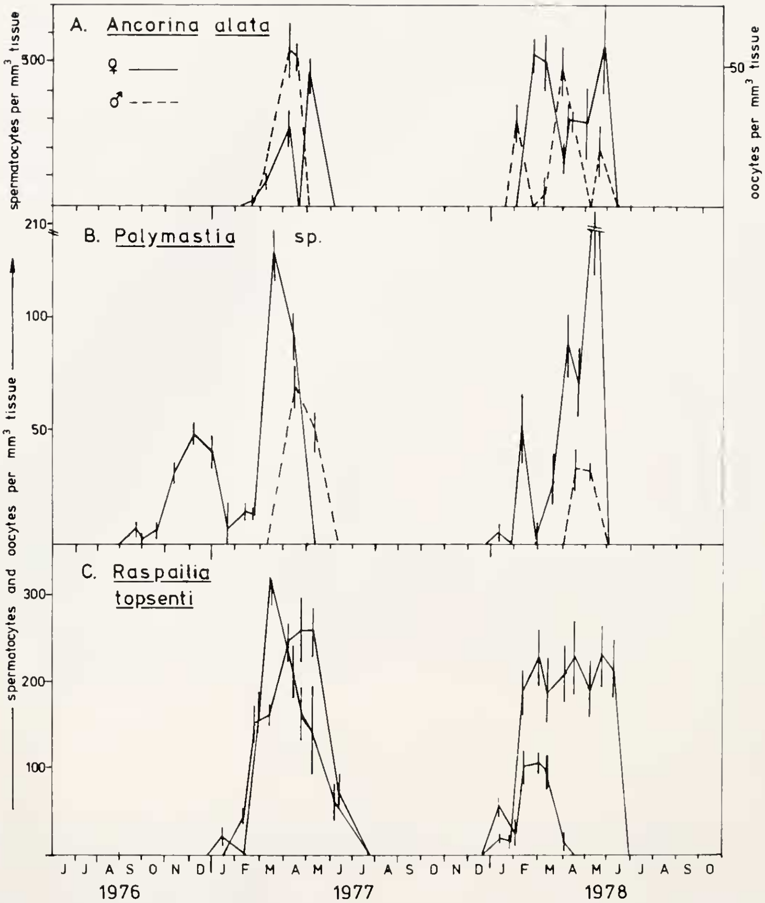

FIGURE 2. Abundance of reproductive elements in three species of discrete sponge. In the graphs of *Ancorina alata* and *Polymastia* sp. the results from one female and one male are shown while for *Raspailia topsenti* that of two females is shown. Vertical lines represent plus or minus one standard error of the mean.

as active. This latter percentage, however, was not taken at the end of the reproductive period and therefore does not include males.

Polymastia sp. is oviparous and apparently gonochoric. Regularly sampled individuals maintained their sexual identity over 2 years. The sex ratio of males to females was 1 : 1.09. Oocytes gradually increased in number over 6 months. Then sperm were produced in the last month of the reproductive period and both gametes released in the last week. Oocytes were always found in groups of two or three and occurred in numbers of up to 130 per mm³ tissue, while sperm appeared to fill large areas of the sponge body though the number of cysts was low: about 60 per mm³ tissue (Fig. 2B). Oocytes were extruded in adhesive masses containing 70 or more elements. Similar adhesive substances were noted by Borojević (1967) around the eggs of *P. robusta*.

Polymastia sp. also produced asexual buds from December to February in 1975–1976 and 1976–1977 but none over the summer of 1977–1978. Buds were approximately 5 mm in diameter and a single large *Polymastia* sp. might have as many as 17 buds at one time, which could be released at a rate of 0.2–4.9 per week per 100 cm^2 surface tissue.

Polymastia hirsuta. This maroon-colored spherical sponge, which may grow up to 15 cm in diameter, was uncommon in the "sponge garden." *Polymastia hirsuta* reproduced over the winter months from late May or June to July or October. In 1976 the regularly sampled sponges produced only oocytes, so in the following year three extra sponges were sampled for spermatocytes. One of these produced sperm. However, two sponges from the original group did not reproduce in this second year. The same pattern was repeated in 1978. Population samples taken in 1977 showed that at least 48% ($N = 50$) of sponges were active and in 1978 at least 80% ($N = 30$).

Polymastia hirsuta is apparently gonochoric and oviparous. The regularly sampled reproducing individuals maintained their sexual identity over the 3-year study period. Oocytes were accumulated over 4 months and sperm produced only in the last month of the reproductive period. Then both gametes were released over 2 weeks. Oocytes and spermatocytes were found throughout the sponge body in numbers of up to 30 per mm^3 tissue. The ratio of males to females was 1 : 1.99.

Aaptos aaptos. This abundant species is a small brown globe sponge supported on a thick pedicel, up to 10 cm in height and with a head diameter of up to 8 cm. The reproductive period of *Aaptos aaptos* was short—from September to October. As none of the continuously sampled sponges reproduced in 1976 a further sample of six individuals were also followed in the next year. Out of the new series one sponge reproduced and again was the only one to reproduce in 1978. In both years this sponge produced oocytes. In the population samples only 22.6% ($N = 92$) of individuals were active in 1977 and 36% ($N = 30$) in 1978. In the "sponge garden" only females were active in 1977, but at Outer Waterfall Reef (5 km from the "sponge garden") in the same year the ratio of males to females was 1:8.3. In 1978, males were sexually active in the "sponge garden" in a ratio of 1 : 1.8, males to females. These data and the evidence from the single regularly sampled sponge that reproduced suggest that *A. aaptos* is gonochoric. However, further sampling of marked individuals is necessary to establish the form of sexuality in this species. Sarà (1961) also suggests that this oviparous sponge is gonochoric. In the present study oocytes were found in numbers of up to 150 per mm^3 tissue and spermatocytes, often in groups, in numbers of up to 170 per mm^3 tissue.

Aaptos aaptos also produced asexual buds from February to April in 1977 but not in 1978. Buds were 2.0–5.0 mm in diameter and produced by 27% of the population at a rate of two per sponge per month.

Polymastia sp. (yellow). This small yellow sponge was the most abundant species of sponge in the "sponge garden" and consisted of a thin base from which arose slender oscule turrets up to 3 cm in height. Sexual products were found in the population in only three instances, once in April, 1977, and twice in January, 1978. Only oocytes were found and these occurred in the basal tissues in numbers of up to 220 per mm^3 tissue.

The major form of reproduction in *Polymastia* sp. (yellow) was the almost year-round production of small buds, which were produced from the tips of the fingers, sometimes in long beads that included the entire oscule turret. Buds were 1.0 mm in diameter and released at a rate of one per finger per month. Only

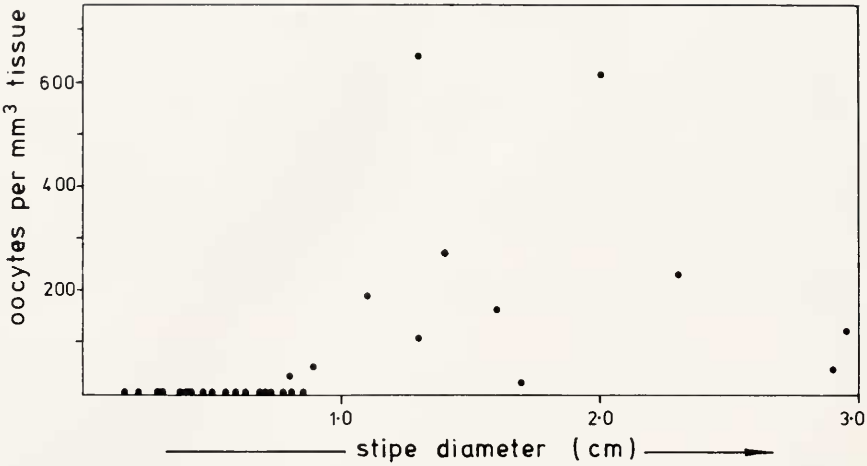

FIGURE 3. Relationship of reproductive activity to size in *Raspailia topsenti.*

13% of the regularly monitored sponges ($N = 30$) produced buds and the mean number of buds released was slightly higher in summer.

Raspailia topsenti. Small individuals of this abundant orange finger sponge consist of a single finger. Larger sponges may have as many as 60 fingers and grow to 30 cm in height. The reproductive period of *Raspailia topsenti* extended from the first weeks of January to the beginning of June. In 1977 four sponges of the regularly sampled group reproduced; in 1978 five of these reproduced. In the first year at least 34% ($N = 35$) of the population reproduced, in the second year 45% ($N = 31$) reproduced. No spermatocytes were found in the populations of this species at the "sponge garden" or at Outer Waterfall Reef. Oocytes were found in numbers of 320 per mm^3 in the fingers of the sponges (Fig. 2C). No sexual products were found in the pedicel or base tissues. There appeared to be a minimum size for the onset of reproductive ability in *R. topsenti,* as sponges of only one or two fingers and a pedicel diameter of less than 0.8 cm did not reproduce. Above this minimum size no relationship was found between size and the number of oocytes present (Fig. 3). After 6 months the oocytes disintegrated in a manner similar to that described by Gilbert (1974). Related species *Axinella damicornis* and *A. verrucosa* were found to be gonochoric and oviparous (Siribelli, 1962).

Settlement and recruitment of sponge larvae

The viviparous larvae of the thinly encrusting sponges took from 1–4 days to settle, while the oviparous larvae of *Polymastia* sp. took from 15–20 days to settle. All larvae crawled the entire time of their mobile lives, unlike many intertidal species which swim for various periods (Bergquist *et al.*, 1970). The viviparous larvae did not travel far after release and large sponge patches could be observed surrounded by settled larvae.

The settlement and recruitment of the larvae from the thinly encrusting sponges in "beach canyon" is recorded in Figure 4. The initial settlement of larvae from *Stylopus* sp. and *Stylopus* sp. (pink) is considered together as they were indistinguishable at that stage. Although large numbers of larvae settled on all monitored surfaces, successful recruitment occurred only on the natural crustose coralline surface. Only two *Stylopus* sp. and five *Stylopus* sp. (pink) survived over the 2 years. *Chondropsis* sp. also settled in large numbers but only 11 survived over the 2 years, again on natural surfaces. The larvae of *Anchinoe* sp. did not settle on any monitored surfaces, perhaps because no monitored areas were near patches of this species.

The recruitment rate of discrete sponges into the "sponge garden" was very low. *Polymastia* sp. (yellow) had the highest recruitment rate, at 0.6 per 0.0625 m^2 area natural habitat per year. Few individuals were recruited into the populations of the other species. Only one new individual each of *Polymastia* sp. and *Polymastia hirsuta* were recruited into the natural habitat. Unattached buds from *Polymastia* sp. could be observed especially over summer but none attached themselves to monitored surfaces.

Discussion

The reproductive patterns of the 10 subtidal species of sponge investigated here show several general features. Two basic patterns were evident: the thinly encrusting ceractinomorphs, which were hermaphrodites producing large viviparous larvae; and the discrete tetractinomorphs, which were gonochoric over

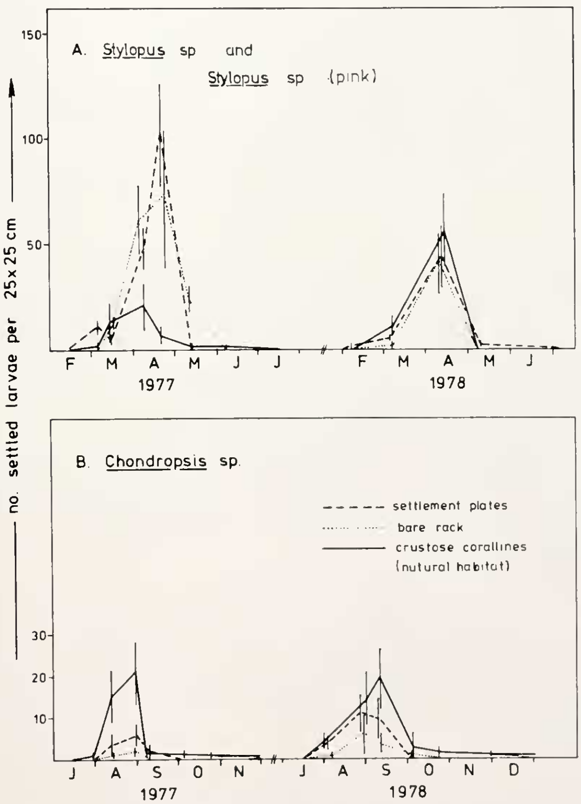

FIGURE 4. Settlement of the larave of *Stylopus* sp., *Stylopus* sp. (pink) and *Chondropsis* sp. on various surfaces. Vertical lines represent plus or minus one standard error of the mean.

2 years and apparently oviparous. Although the information collected is suggestive of the latter form of sexuality in *Raspailia topsenti*, *Aaptos aaptos*, and *Polymastia* sp. (yellow) further data are necessary to establish this conclusively. However, in general these data support the taxonomic division of the Demospongiae proposed by Lévi (1957) into the viviparous subclass Ceractinomorpha and the oviparous Tetractinomorpha.

The potential reproductive output of each viviparous species was different and some relationship of this to the abundance of the species was indicated. The small uncommon species *Anchinoe* sp. (also *Hymedesmia* sp. [red] and *Microciona* sp.; unpublished data) produced large numbers of larvae while the larger, spreading, abundant species such as *Stylopus* sp. and *S.* sp. (pink) produced fewer larvae. *Chondropsis* sp., although uncommon in the "beach canyon" area, produced few but much larger larvae than any of the other species.

In the reproductive patterns of the discrete species there appeared to be a relationship between length of reproductive period and release of gametes. Sponges such as *Ancorina alata* and *Aaptos aaptos* had short reproductive periods in which sperm and oocytes were produced simultaneously. In *Polymastia* sp. and *Polymastia hirsuta* oocytes were gradually accumulated over a long period. Then sperm were produced at the end of the reproductive period and released simultaneously with oocytes. In the discrete sponge populations there were few males. The males of *Aaptos aaptos* in the "sponge garden" were reproductively active in only 1 year of the study, suggesting that some of the non-reproductive members of the population are males. Thus the apparent sex ratio of the species can change each year. However, in general it appears that in sponge species there is usually a higher percentage of females reproductively active in the population than males (Hogg, 1967; Fell, 1976b; Johnson, 1978).

In both years of the study a percentage of each species population did not reproduce sexually. This non-reproductive percentage was not related to the sponges' ages, except in the case of *Raspailia topsenti* and *Aaptos aaptos*, but may have been related to temperature changes. In the second year of the study higher water temperatures were recorded than in the previous year and during this period a greater percentage of the population of each species was reproductively active. Such changes may have been due to temperature-related differences in food levels. Johnson (1978) found that habitat also affected the number of individuals reproducing in any year.

The different reproductive strategies appeared to be related to the level of disturbance the sponges normally encountered. The two sponge communities studied were subject to different intensities of disturbance. The thinly encrusting species in "beach canyon" were subject to the highest intensity of disturbance not only from urchins, which grazed 5% of the surface per year (A. L. Ayling, 1978a), but from surge produced by storms. An abundant leatherjacket fish (*Parika scaber*) also removed newly settled larvae (A. M. Ayling, 1976). In the "sponge garden" the overlying sediment made it impossible for urchins to graze or leatherjackets to graze effectively. Disturbance in this area was low and the only predators were opistobranchs, which were rare and which specialized on a few species of sponge.

The reproductive strategy of the thinly encrusting sponges living in the area of highest disturbance was to produce large larvae capable of rapid settlement and growth to sizes capable of withstanding grazing. Sponges that had reached 0.5 cm in diameter could be almost completely scraped off the substratum but still be able to reoccupy the lost space (A. L. Ayling, 1978a). Stimson (1978) has suggested that viviparous planulae of corals are adaptations for rapid settlement in fast-moving waters. The oviparous larvae of discrete sponges, on the other hand, were up to a 100 times more numerous (as determined from the potential output inside the sponge) than the viviparous larvae of the thinly encrusting species. But they were small and it appears that they may also crawl for long periods of time (Borojević, 1967; Bergquist *et al.*, 1970).

On release, subtidal viviparous larvae did not disperse widely but settled close to the parent sponges. The dispersion patterns of the discrete sponges (A. L. Ayling, 1978a) suggests that this may also be true of their larvae, but further work is needed. Such aggregated dispersion patterns produced by the settling larvae of subtidal sponges suggests that more detailed documentation of settlement patterns is needed than that currently obtained from a few randomly placed settlement plates or shells.

Settlement of larvae occurred on all surfaces but recruitment was most successful in the natural habitat. Sutherland and Karlson (1977) found that sponge larvae were common invaders of "mature" assemblages in epibenthic communities. Recruitment of sponge larvae on their ceramic tiles was very unpredictable. In the present study subtidal sponges reproduced regularly each year but the number of larvae surviving was unpredictable and generally low. In *Polymastia* sp. (yellow), however, the continuous production of buds ensured a predictable but low recruitment of individuals each year.

I wish to thank Dr. P. R. Bergquist for her help and criticism during this work. For many useful discussions I would like to thank Dr. Howard Choat and David Schiel. Maureen Fischer gave me invaluable assistance with histological preparations. Tony Ayling discussed and criticised the manuscript with me. Support for this work was provided by the Roche Research Institute of Australia.

Summary

1. The patterns of sexuality and asexual reproduction in 10 species of subtidal Demospongiae were investigated by following reproductive activity in particular individuals and in the populations of each species over a 2-year period. Potential reproductive output was measured and related to recruitment rates recorded from natural and artificial surfaces.

2. The ceractinomorph sponges were found to be all hermaphrodites producing viviparous larvae while most of the tetractinomorph sponges were found to be gonochoric over the period of study and apparently oviparous. In the tetractinomorph sponge populations there was usually a majority of females and in two species no males were found. Three of the tetractinomorph species also produced buds.

3. Viviparous larvae are thought to be adaptations to habitats with high levels of disturbance.

4. Recruitment in both groups of sponges was low and unpredictable except in *Polymastia* sp. (yellow) which produced buds all year round and had predictable recruitment of low numbers of individuals. Recruitment occurred predominantly on natural surfaces.

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